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Polytypic species of pronophiline butterflies in the subpáramo and páramo of the Venezuelan Cordillera de Mérida I: Distribution patterns and affinities of *Lymanopoda marianna* STAUDINGER based on morphological and molecular data  
(Lepidoptera: Nymphalidae: Satyrinae)

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**ABSTRACT:** *Lymanopoda marianna* STAUDINGER (Nymphalidae, Satyrinae) is an endemic species of butterfly of the Venezuelan Cordillera de Mérida. It was hitherto considered monotypic, however this study shows it is highly polytypic. Five new subspecies are described differing noticeably in the shape, size and colour of the conspicuous hindwing upperside bluish-green patch. Some differences can be observed in male genitalia as well. A western-eastern slopes biogeographical pattern is uncovered, and the Santo Domingo Valley is recognized herein for the first time as a center of endemism at a subspecies level. Microstructure and function of hindwing upperside blue scales are discussed suggesting their role in mate locating. Affinities and phyletic relations of *L. marianna* with other congeners are discussed based on colour patterns, male and female genitalia, and molecular data. Male genitalia and molecular data place it in the clade of *L. obsoleta* however female genitalia and colour patterns indicate close affinity with *L. lebbaea/L. labda*, distantly related according to molecular phylogeny.

**Key words:** entomology, taxonomy, El Batallón, biogeography, colour patterns, female genitalia, *Lymanopoda marianna giselleae* ssp. n., *L. marianna ioanae* ssp. n., *L. marianna jacquelineae* ssp. n., *L. marianna valentinae* ssp. n., *L. marianna veronicae* ssp. n., male genitalia, molecular phylogeny, Santo Domingo, subpáramo.

**RESUMEN:** *Lymanopoda marianna* STAUDINGER - especie endémica de mariposa (Nymphalidae, Satyrinae, Pronophilini) de la Cordillera de Mérida en Venezuela, considerada hasta ahora como monotípica - demuestra ser altamente politípica. En este estudio se describen

cinco nuevas subespecies que difieren inmediatamente por la forma, el tamaño y el color de la conspicua mancha azul-verde de la cara dorsal de las alas posteriores. Algunas diferencias se pueden observar también en la estructura de los genitales masculinos. Se evidencia un patrón biogeográfico este-oeste y se reconoce al valle de Santo Domingo por primera vez como un centro de endemismo a nivel de subespecie. Se examinan las microestructuras y las funciones de las escamas azules de la cara dorsal de las alas anteriores, sugiriendo su rol en el apareamiento. Se discuten las afinidades y las relaciones filéticas de *L. marianna* con otras especies del género basado en datos morfológicos, patrones alares, genitales masculinos y femeninos, y moleculares. Los genitales masculinos y los datos moleculares ubican a *L. marianna* en el clad de *L. obsoleta* sin embargo los genitales femeninos y el diseño alar indican un parentesco cercano con *L. lebbea*/*L. labda* especies poco relacionadas de acuerdo con la filogenia molecular.

Palabras clave: Batallón, biogeografía, filogenia molecular, genitalia femeninos y masculinos, *Lymanopoda marianna giselleae* ssp. n., *L. marianna ioanae* ssp. n., *L. marianna jacquelineae* ssp. n., *L. marianna valentinae* ssp. n., *L. marianna veronicae* ssp. n., patrones de coloración, Santo Domingo, subpáramo.

#### INTRODUCTION

ADAMS & BERNARD's (1981) article "Pronophilina butterflies of the Venezuelan Cordillera de Mérida" remains the main general reference to the fauna of the tribe Pronophilini (Nymphalidae, Satyrinae) in this Andean range. Even though its title implies a study dedicated to the entire Cordillera de Mérida, it is in fact geographically restricted to the central part of the range, the valley of the Río Chama, with no data from other areas. Also, the results presented by ADAMS & BERNARD (*op. cit.*) are somewhat misleading, suggesting that the fauna of the Chama valley is representative for the entire Cordillera de Mérida. This appeared inaccurate in the light of subsequent studies, which revealed the presence of endemic species and subspecies of the genera *Diaphanos* ADAMS & BERNARD (VILORIA 1994), *Steromapedaliodes* FORSTER (VILORIA & PYRCZ 2002), *Redonda* ADAMS & BERNARD (VILORIA *et al.* 2003) and *Pedaliodes* BUTLER (PYRCZ & VILORIA 2009) in other parts of the Cordillera de Mérida. The most recent field studies show that the above mentioned contributions merely uncovered the tip of an iceberg, demonstrating that the distribution patterns of Pronophilini in this part of the Andes are more intricate, and that faunistically the Cordillera de Mérida is heterogenous.

This paper is the first in a series dedicated to the zoogeography, taxonomy and phylogeny of Satyrinae species inhabiting the páramos and subpáramos of the Cordillera de Mérida belonging to the genera *Redonda*, *Steromapedaliodes*, *Diaphanos*, *Cheimas* STAUDINGER, *Corades* HEWISTON and *Lymanopoda* WESTWOOD. It is concerned with *Lymanopoda marianna* STAUDINGER (1897). The genus *Lymanopoda* WESTWOOD (1851) placed in the tribe Pronophilini by MILLER (1968) is characterized by at least two synapomorphies of wing colour pattern. FW ocelli in cells Cu1-Cu2 and Cu2-1A are always displaced basally in relation to remainder. HWV median band is broken, displaced in discal-cell and connected to post basal band, which is a type of distortion of the ground plan ("pierellization" *sensu* SCHWANWITSCH 1924) not apparent in some predominantly white species, in which the underside pattern is simplified (PYRCZ *et*

al. 1999; PYRCZ 2004). Further synapomorphies can be identified in male genitalia, namely a well developed superuncus, which is a bulbous projection of tegumen on the base of uncus; atrophied gnathi adhered to ventral surface of uncus; a (usually) strongly sclerotized sub-scapium; valvae with two prominent sculptured processes on the dorsal surface (in a few cases not apparent). Other possible synapomorphies can be found in female genitalia, such as a sclerotized lamella of anal papillae on the distal part of the posterior apophysis, an accessory gland (probably) producing an egg gluing secretion posterior to the ostium bursae (PYRCZ *et al.* 1999; PYRCZ 2004); a long, usually Y-shaped projection anteriorly to ostium bursae. Phyletic value of female genitalia characters still need to be confirmed. PEÑA *et al.* (2006), in a phylogenetic study based on molecular data place *Lymanopoda* in a monophyletic group alongside *Ianusiusa* PYRCZ, *Tamania* PYRCZ, *Idioneurula* STRAND and *Manerebia* STAUDINGER, refuting the hypothesis that *Manerebia* belongs in the predominantly Holarctic subtribe Erebiina (LAMAS & VILORIA 2003).

#### STUDY AREA

Venezuelan Andes constitute an extension of the Colombian Eastern Cordillera, which bifurcates in the Pamplona Knot into the Sierra de Perijá and the Cordillera de Mérida. The latter is separated from the El Tamá, the northern extremity of the Eastern Cordillera, by the so-called Táchira depression. The highest contact point between the two ranges is at 1000 m. The Cordillera de Mérida extends over 300 km long and 80 km wide in the north-east direction to the Carora (Lara state) and Yaracuy (Yaracuy state) depressions, over an area of about 32500 km<sup>2</sup>. It creates a great divide between the watersheds of the affluents of Orinoco in the south-east, and the Maracaibo Lake drainage in the north-west. The Cordillera de Mérida can be divided into three higher main sections: south-western, central and north-eastern. The south-western section is dominated by the Páramo de Batallón topping at 3913 m, the slightly lower Zumbador and La Negra massifs, and the Sierra de Tovar culminating at the Páramo de Nariño at 3517 m. The central section is the highest, with two parallel ranges separated by the Chama river valley, the Sierra Nevada with the top elevation of Venezuela, the Pico Bolívar at 5007 m, and several peaks reaching above 4500 m, extending towards north-east to the Sierra de Santo Domingo, and the Páramo de La Culata with the highest elevation at the Páramo de Piedras Blancas at 4729 m, extending to the Sierra de Trujillo, with the highest elevation at the Teta de Niquitao, at 4003 m. The northern section is made up by the massifs of Guaramacal and its northern extension the Páramo Cendé at 3650 m.

Montane vegetation of the Cordillera de Mérida is a mosaic of cloud forests covering mostly its outer slopes, sub-desert shrubs in the interandean valleys and páramos above the upper forest limit. The vegetation of páramo consists mainly of bunch grasses, conspicuous giant rosettes such as *Espeletia* (and related genera) and *Puya*, and thick *Polylepis* forests, generally above 3000 m, but locally to 2500 m. In the subpáramo, 2500-3000 m, mosaics with shrubs and small trees alternate with grasslands. Its typical elements are primitive espeletines of the genus *Libanothamnus*, *Blechnum* ferns and

bamboos of the *Chusquea* sub-genus *Swallichloa* (SALGADO-LABOURIAU 1979; VEILLON 1989; JUDZIEWICZ *et al.* 1999). In the northern part of the range, dwarf *Aulonemia* bamboos can be found locally in the subpáramo (JUDZIEWICZ & RIINA 2005).

#### MATERIAL AND METHODS

Field work was carried out by the authors throughout the Cordillera de Mérida in 1991-1992, 1996-1997, 2002 and 2005-2008. Sampled localities are listed in Appendix 2. Collecting of adults was carried out with standard entomological nets and Van-Sommeren traps baited with carnivorous animal dung. Types and comparison material was examined in major European and American museums and private collections specified below. Male genitalia preparations were made according to standard procedures, which is by soaking in hot 10% KOH solution. Dissected parts of male genitalia were preserved in glycerol microvials attached to the specimens and duly labeled. Dissected female genitalia were fixed on euparal transparencies. Morphological terms for genitalia largely follow KLOTS (1956). Head microstructures were examined under an Olympus SZX9 stereomicroscope, and scales under a SEM microscope. Adults were photographed with an Olympus E-500 digital camera and plates were composed with Adobe Photoshop 8.

Molecular data was obtained for two samples of *L. marianna* and 205 other specimens of *Lymanopoda* and *Ianussiusa* PYRCZ. Five protein-coding genes were analyzed, 1 mitochondrial- 1459 bps of cytochrome oxidase subunit 1 (COI), and 4 nuclear- 403 bps of wingless (*wg*), 1054 bps of elongation Factor 1 alpha (EF-1 alpha), 606 bps of ribosomal protein S5 (RPS5), and 691 bps of glyceraldehyde-3-phosphate dehydrogenase (GAPDH)- for a total of 4,213 nucleotides. Analyses were run on individual genes, concatenated nuclear + mtDNA, and all genes concatenated. Sequences were aligned using Sequencher 4.8 and concatenated using Mesquite. MacClade 4.07 was used to define codon positions and genes. The model of evolution was found for each gene and concatenated genes using ModelTest 3.7. Maximum parsimony and maximum likelihood trees using the heuristic search criterion were produced for each gene and combinations of genes using MrBayes 3.1.2. The genus *Ianussiusa* was used as the outgroup. A partial tree based on data from 48 specimens of *Lymanopoda* and one specimen of *Ianussiusa* was produced in order to illustrate the position of *L. marianna* and the relative position of *L. obsoleta* and *L. labda* clades in the phylogeny of *Lymanopoda*. Voucher data are listed in Appendix 3.

The following abbreviations and collection acronyms were used:

- BMNH: The Natural History Museum, London, UK (formerly British Museum, Natural History);
- HMNH: Hungarian Museum of Natural History, Budapest, Hungary;
- IVIC: Instituto Venezolano de Investigaciones Científicas, Caracas, Venezuela;
- MCC: collection of Mauro and Clara COSTA, Caracas, Venezuela;
- MIZA: Museo del Instituto de Zoología Agrícola de la Universidad Central, Maracay, Venezuela;

MZUJ: Muzeum Zoologiczne Uniwersytetu Jagiellońskiego, Kraków, Poland;  
 PBF: collection of Pierre BOYER, Le Puy Sainte Réparate, France;  
 SMTD: Staatliche Museum für Tierkunde, Dresden, Germany;  
 TWP: collection of Tomasz Wilhelm PYRCZ, Warsaw, Poland (to be integrated into MZUJ);  
 UCD: University of California, Davis, USA;  
 ZMHB: Zoologische Museum, Humboldt Universität, Berlin, Germany;  
 CM: Cordillera de Mérida;  
 EC: Colombian Eastern Cordillera;  
 FW: Forewing;  
 HW: Hindwing;  
 D: Dorsum;  
 V: Venter.

## SYSTEMATIC OVERVIEW

*Lymanopoda marianna marianna* STAUDINGER, 1897

(FIGS. 1A, 2E, 6C)

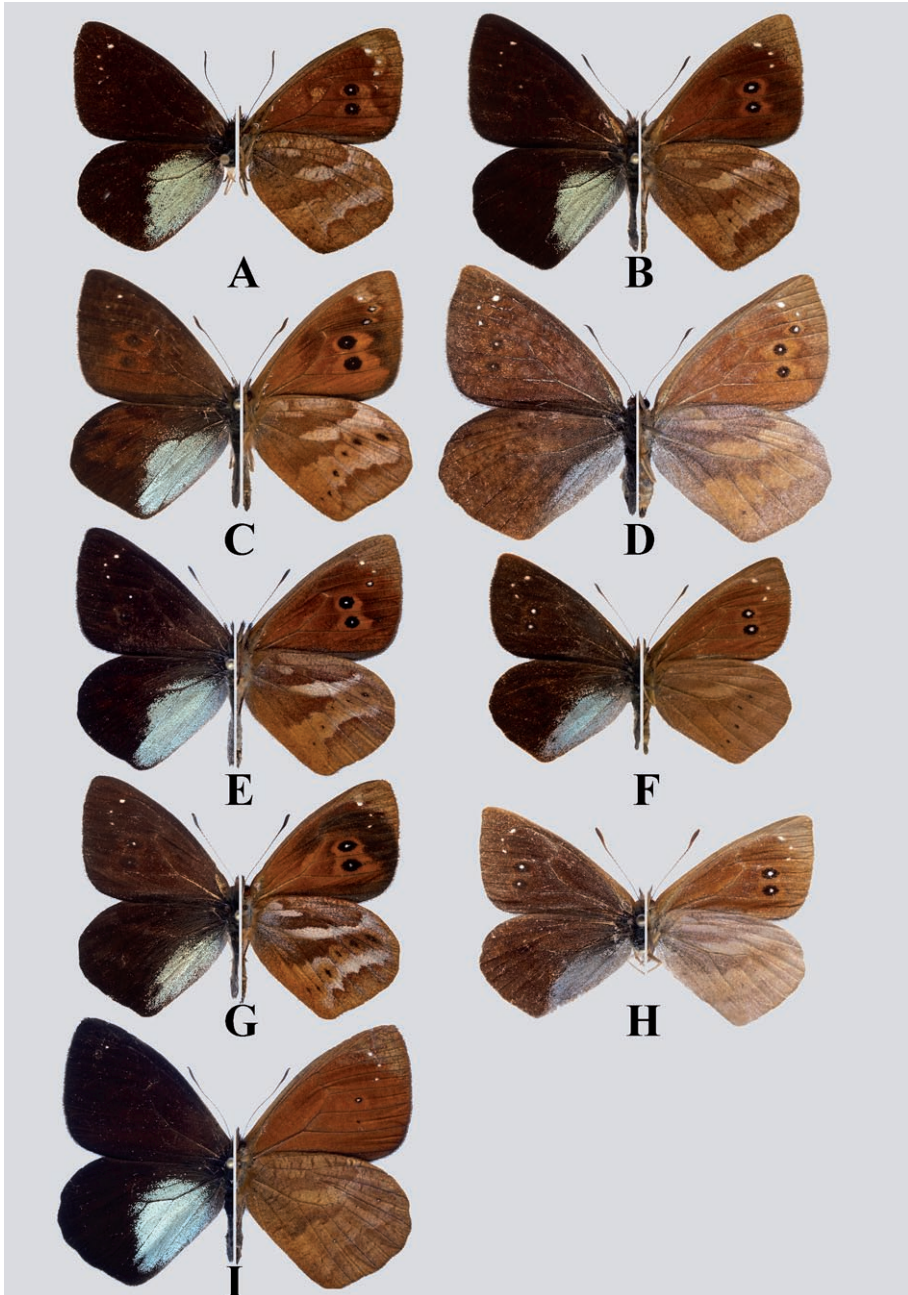
*Lymanopoda marianna* STAUDINGER, 1897: 146, pl. 5, fig. 6 (male).*Lymanopoda marianna* STAUDINGER; WEYMER 1911: 246, pl. 52 row f; GAEDE 1931: 486; ADAMS & BERNARD 1981: 358, fig. 6 (male genitalia); D'ABRERA 1988: 818, fig. (male); PYRCZ, WILLMOTT & HALL 1999: 498; LAMAS, VILORIA & PYRCZ 2004: 210.

## MATERIAL EXAMINED

1 ♂: Mérida, Venezuela, [ZMHB] (lectotype, selected by L. D. MILLER in 1989, designation of the lectotype unpublished) herein designated (red rectangular label, black ink markings); 1 ♂: same data (paralectotype), herein designated (red rectangular label, black ink markings); 1 ♂: Mérida; 1 ♂: no locality, *ex coll.* Rothschild; 1 ♂: Venezuela, Rio Albarregas, 3050 m, *ex coll.* Adams & Bernard Colombia 1978 – 310; 1 ♂: Mérida, *ex coll.* Grose-Smith; 1 ♂: Mérida; 1 ♂: Venezuela, *ex coll.* Fruhstorfer; 1 ♂: Albarregas, 3050 m, *leg.* G. Bernard, 1977, [BMNH]; 1 ♂: Mérida, Venezuela, 1914, *leg.* Alex Heyne, [MNHN]; 1 ♂: Mérida, La Culata, 1992, T. Pyrcz *leg.*, [MALUZ]; 1 ♂: Mérida, La Culata, Alto Rio Mucujún, 3050-3100 m, 03.IV.2006, P. Boyer *leg.*, [PBF]; 1 ♂: Mérida, La Culata, 3000 m, 01.IV.1992, T. Pyrcz *leg.*, [TWP]; 1 ♂: Mérida, La Culata, Alto Rio Mucujún, 3050-3100 m, 03.IV.2006, T. Pyrcz *leg.*; 1 ♂: same locality, 3400-3450 m, 06.II.2007, T. Pyrcz *leg.*; 1 ♂: Sierra Nevada, above La Aguada, 3550 m, 02.II.2007, T. Pyrcz *leg.*, [TWP].

## REDESCRIPTION

MALE (Fig. 1A): Head: Eyes chocolate brown, hairy; antennae reaching to 2/5 the length of costa, blackish brown, shaft with white scales at base of each segment, club twice as thick as shaft, flattened; palpi twice the length of head, dirty yellow, covered with yellow and grey scales. Thorax: dorsally blackish brown, ventrally covered with thick yellowish hair. Abdomen: dorsally and laterally blackish brown, ventrally light



1. Adults (left: dorsum/right: venter): A. *Lymanopoda marianna marianna* male (La Culata); B. *Lymanopoda m. valentinae* male (holotype); C. *Lymanopoda marianna giseleae* male (holotype); D. *Lymanopoda m. giseleae* female (paratype); E. *Lymanopoda m. veronicae* male (holotype); F. *Lymanopoda m. veronicae* female (paratype); G. *Lymanopoda m. ioanae* male (holotype); H. *Lymanopoda m. ioanae* female (paratype); I. *Lymanopoda m. jacquelineae* male (holotype)



grey. Wings: Forewing apex subacute, outer margin straight. Hindwing oval with a smooth outer margin and tornus at straight angle. Forewing length: 21-23 mm, mean: 22.3 mm, n=9. Forewing upperside uniform blackish-brown, turning a shade lighter in older individuals; white subapical dots not apparent in the examined individuals. Hindwing upperside ground color blackish-brown; a shining golden-greenish patch, entering discal cell and reaching to tornus, although not extending over distal margin. Forewing underside ground color chocolate brown with a light orange overcast; apical area dusted with beige; three white subapical dots as on the upperside; two black postmedian ocelli in M3-Cu1 and Cu1-Cu2 with white pupils and an orange halo spreading to tornus and distal margin. Hindwing underside ground color beige-brown, with a delicate ripple-like pattern of darker scales on the entire wing surface; a lighter postmedian to submarginal band with a notch entering lower half of discal cell and a row of six minute dots aligned in a shallow curve pointing basally. (Translation of the original German description in Appendix 1). **Male genitalia** (Fig. 2E, 6C): Superuncus prominent, 2/3 the length of uncus; uncus stout, slightly curved downwards; gnathos short and adhered to base of uncus; sub-scapium heavily sclerotized; saccus flattened of intermediate depth; valvae elongated with two long, thin and straight processes, both dentate towards tip only and of similar length; aedeagus straight, spines towards apical 1/4, about the length of valva+saccus.

FEMALE: Hitherto unknown.

*Lymanopoda marianna valentinae* PYRCZ, n. ssp.

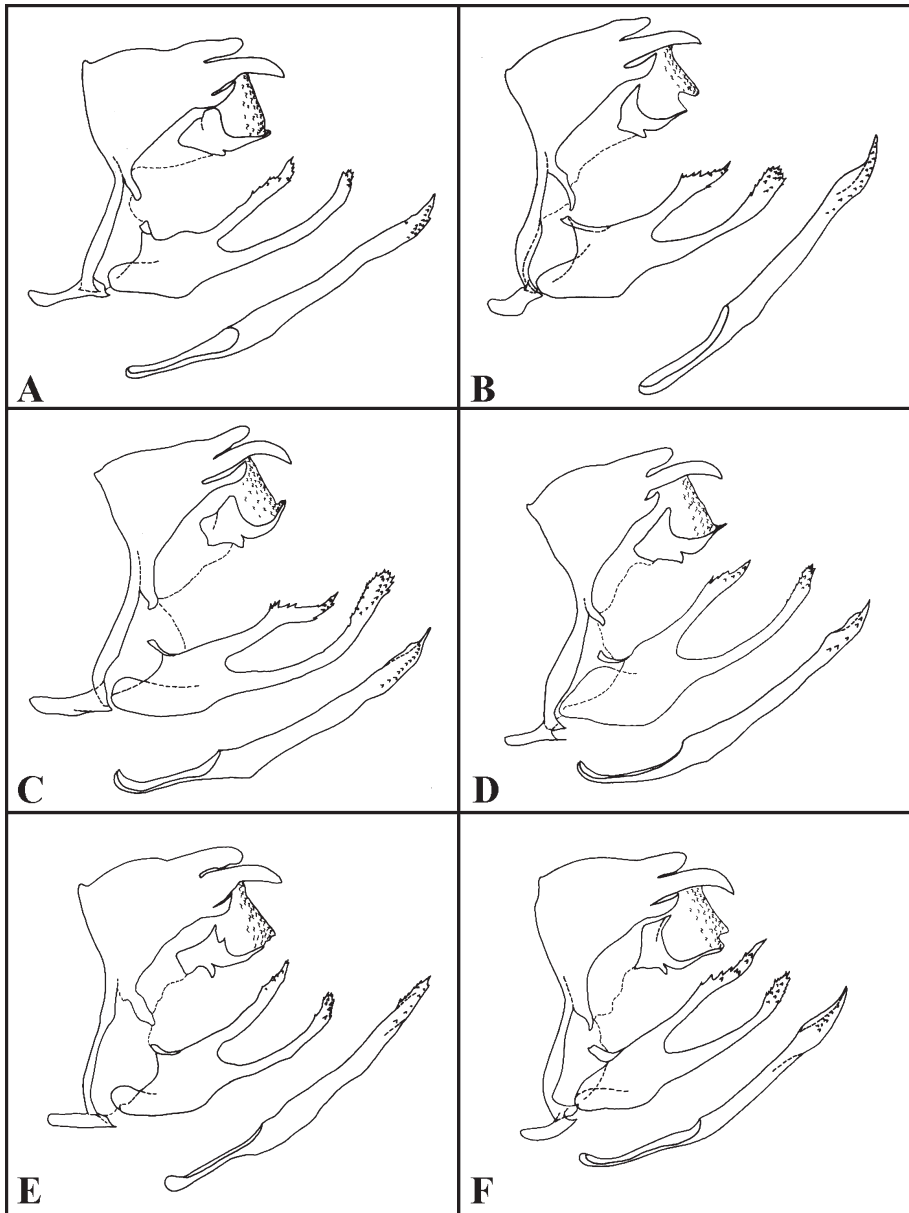
(Figs. 1B, 2F, 3D)

TYPE MATERIAL

HOLOTYPE ♂: Venezuela, Edo. Mérida, Pueblo Llano – Tuñame, Qda. Ranchería, 2900-2950 m, 27.XI.2005, T. Pyrcz *leg.*, [MIZA]; Paratypes (35 ♂♂): same data as the holotype, 10 [MZUJ], 10 [TWP]; 2 ♂: Mérida, Pueblo Llano vers Niquitao, 2km après Ranchería, 2850 m, 25.II.2005; P. Boyer *leg.*; 12 ♂♂: same data but 27.II.2005, [PBF]; 1 ♂: Mérida, Mucubají – Santo Domingo, Los Frailes, 2900-2950 m, 09.IV.2006, T. Pyrcz *leg.*, [TWP].

DESCRIPTION

MALE (Fig. 1B): Head, thorax and abdomen as in the nominate subspecies. Wings: Slightly smaller than *jacquelineae*, same size as the nominate but larger than *veronica* and *ioanae*: forewing length: 20-23 mm, mean: 21.5 mm, n=36. Forewing upperside uniform blackish-brown, turning a shade lighter in older individuals, same as in the nominate; three minute, white subapical dots in R5-M1, M1-M2 and M2-M3, and a white postdiscal dot in M3-Cu1, apparent in all examined individuals of *valentinae*, although in some cases barely noticeable, absent in most specimens of the nominate. Hindwing upperside ground color blackish-brown, same as in the nominate subspecies; a shining greenish patch, similarly colored as in the nominate subspecies, although in some individuals with a light bluish sheen, entering discal cell, as in the nominate subspecies, but noticeably shorter along the anal margin ending at 2/3 to 3/4 the distance to



2. Male genitalia (in lateral view, aedeagus removed from its natural position): A. *Lymanopoda marianna giseleae* (paratype); B. *Lymanopoda m. jacquelineae* (paratype); C. *Lymanopoda m. veronicae* (paratype) D. *Lymanopoda m. ioanae* (paratype); E. *Lymanopoda m. marianna* (Alto Rio Albarregas); F. *Lymanopoda m. valentinae* (paratype)



tornus, whereas it extends to tornus or nearly so in the nominate. Forewing underside ground color slightly darker than in the nominate subspecies, chocolate brown with a light orangey overcast; apical area dusted with beige; three white subapical dots as on the upperside; two black postmedian ocelli in M3-Cu1 and Cu1-Cu2 with white pupils and an orange halo, more restricted than in the nominate subspecies. Hindwing underside ground color beige-brown, slightly lighter and duller than in the nominate subspecies, with a delicate ripple-like pattern on the entire wing surface also noticeable in the nominate subspecies; otherwise similar to other subspecies. **Male genitalia** (Fig. 2F): Superuncus slightly shorter than in the nominate subspecies, valvae a fraction longer, thinner and with the tip somewhat more hooked; gnathos similar; sub-scapium heavily sclerotized; saccus slightly deeper than in the nominate subspecies; spines on the dorsal process more prominent than in the nominate subspecies, reaching to its half length, with the tip pointed, exceeding the length of ventral process; aedeagus similar to the nominate subspecies.

**FEMALE:** Two females were observed but not collected; therefore they are not available for the description.

#### ETYMOLOGY

This subspecies is dedicated to Nadia Valentina Sánchez RACHAUS, a sister in law of the senior author.

#### *Lymanopoda marianna jacquelineae* PYRCZ, n. ssp.

(Figs. 1I, 2B)

Type material: HOLOTYPE ♂: Venezuela, Edo. Mérida, Paso Aguila – Piñango road, Km 26, Sector El Potrero, 2900-2950 m, 09.IV.2006, T. Pyrcz *leg.*, [MIZA]; Paratypes (9 ♂♂): same data, 3 [TWP], 3 [MZUJ]; 3 ♂: Mérida, via El Aguila a Piñango km26, "Potrero", 3200/3300m, 8.IV.2006, P. Boyer *leg.*, [PBF].

#### DESCRIPTION

**MALE** (Fig. 1I): Head, thorax and abdomen as in the nominate subspecies. Wings: Characterized by the larger size than other subspecies: forewing length: 22.5-24 mm, mean: 22.9 mm, n=10. Forewing upperside uniform blackish brown, a shade darker than in other subspecies; contrary to other subspecies, subapical white dots absent in all except one examined individuals. Hindwing upperside ground color blackish brown, same as on the forewing; shining patch bluish green, same as in most individuals of *valentinae*, large, covering half of discal cell and almost reaching tornus, shaped as in the nominotypical. Forewing underside almost uniform brown-brick red; costal and apical areas dusted with beige; three tiny, whitish subapical dots in R4-R5 to M2-M3; two postmedian black ocelli pupiled with white minute or barely visible, noticeably smaller than in other subspecies. Hindwing underside sandy yellow liberally dusted with beige and brick red, generally without any well-defined pattern, in a few examined individuals faint, darker basal to median areas, except in discal-cell, and between sub-marginal line and outer margin. **Male genitalia** (Fig. 2B): Superuncus slightly shorter

than in the nominate subspecies and *giselleae*, valvae a fraction thinner and; gnathos similar to other subspecies; sub-scapium heavily sclerotized; saccus shallower than in the nominate subspecies or *giselleae*; spines on the dorsal process more prominent than in other subspecies, similar to *veronica*, reaching to its half length, shorter than ventral process, the latter noticeably thicker in distal half; aedeagus similar to the nominate and other subspecies.

FEMALE: Hitherto unknown.

#### ETYMOLOGY

This subspecies is dedicated to the senior author's wife, Jacqueline SÁNCHEZ-PYRCZ.

### *Lymanopoda marianna giselleae* PYRCZ, n. ssp.

(Figs. 1C, 1D, 2A)

#### TYPE MATERIAL

HOLOTYPE ♂: Venezuela, Edo. Mérida, El Hatico Range, El Baho, La Ciénaga, 2900-2950 m, 21.XI.2005, T. Pyrcz leg., [MIZA]; Paratypes (22 ♂♂ and 1 ♀): 1 ♂: same data as the holotype; 2 ♂♂: El Baho – via El Páramo, 2950 m, [TWP]; 2 ♂♂: El Baho, via El Páramo, 2900-2950 m, 26.XI.2005, T. Pyrcz leg.; 1 ♂: same data but 3000 m, [MZUJ]; 1 ♀: same data but 3150 m, P. Boyer leg., [TWP]; 4 ♂♂: Edo. Barinas, Los Morritos, 3000 m, 06.I.2006, J. Clavijo leg., [MIZA]; 2 ♂♂: Edo. Barinas, Los Morritos, 3000 m, 06.I.2006, M. Costa leg., 1 [MCC], 1 [TWP]; 1 ♂: Edo. Mérida, Paramo de San José (eastern slopes), 2800 m, 12.II.2007, T. Pyrcz & K. Anderson leg., [TWP]; 3 ♂♂: Mérida, El Baho, Santo Domingo vers Apartaderos km 4, 2850/3100 m, 21.XI.2005, P. Boyer leg.; 4 ♂♂: same data but 26.XI.2005, P. Boyer leg.; 1 ♂: same data but 28.I.2008, P. Boyer leg.; 1 ♂: Mérida, Páramo de San José, 3100 m, 20.II.2008, [PBF].

#### DESCRIPTION

MALE (Fig. 1C): Head, thorax and abdomen as in the nominate subspecies. Wings: Same size as the nominate and *valentinae*, slightly smaller than *jacquelineae*, but larger than *veronica* and *ioanae*; forewing length: 20-24 mm, mean: 21.5 mm, n=15. Forewing upperside ground color dark brown, slightly lighter than in the nominate or other subspecies, not uniform but with lighter patches reflecting the pattern of the underside, particularly noticeable in fresh individuals; between one and four white subapical dots in R4-R5 to M2-M3, in some individuals well marked, in others faded; two black post-median ocelli, barely visible on the ground color, in M3-Cu1 and Cu1-Cu2, in some individuals with minute, barely visible white pupils. Hindwing upperside ground color same as on the forewing, similarly with a pattern of lighter brown patches; a shining light blue patch, in some individuals with a light greenish shade, marginally entering discal cell and extending to tornus along anal margin, approximately the same size as in the nominate and larger than in *valentinae*, with a diffuse inner margin. Forewing underside ground colour varying between russet and dark brown; with an orange or

russet-brown suffusion around postmedian ocelli in M3-Cu1 and Cu1-Cu2, in some specimens extending into postmedian area, similar to the nominate subspecies; a greyish-white subapical suffusion, lighter and more noticeable than in other subspecies, inclosing three whitish subapical dots; apical area chestnut. Hindwing underside color pattern more contrasting than in the nominate or *valentinae*, with the median area and outer half of discal cell lustrous whitish-beige, in some specimens with a prominent grey-white suffusion, basal area chocolate brown and the border between the two areas sharply defined; a fine, darker brown ripple-like pattern similar to the nominate and *valentinae*. **Male genitalia** (Fig. 2A): Superuncus, valvae and gnathos similar to the nominate subspecies; sub-scapium heavily sclerotized; saccus slightly deeper; dorsal process of the valvae slightly shorter than ventral, spines on the ventral process small and restricted to the tip; aedeagus similar to the nominate subspecies.

**FEMALE** (Fig. 1D): Forewing length: 24 mm. FWD and HWD chestnut, lighter than the male, and considerably lighter than the females of other subspecies; subapical white dots, and postmedian black, white pupiled ocelli in M3-Cu1 and Cu1-Cu2 apparent; forewing underside chestnut with a prominent sandy yellow suffusion; hindwing underside light brown with a prominent sandy yellow suffusion, not apparent in other subspecies, and a fine grey scaling especially in basal, median and marginal areas. **Female genitalia**: not examined.

#### ETYMOLOGY

This subspecies is dedicated to Giselle Karin SÁNCHEZ, a sister in law of the senior author.

### *Lymanopoda marianna veronicae* PYRCZ, n. ssp.

(Figs. 1E, 1F, 2C, 7C1, 7C2, 3C)

#### TYPE MATERIAL

**HOLOTYPE** ♂: Venezuela, Edos. Mérida – Táchira border, Bailadores – Pregonero, Mesa Alta, 2900-2950 m, 03.XII.2005, T. Pyrcz leg., [MIZA]; Paratypes (43 ♂ and 2 females): 32 ♂♂: same data as the holotype, 16 [MZUJ], 16 [TWP]; 1 ♂: Edo. Mérida, Bailadores – Pregonero, Qda. de Los Píos, 2900-2950 m, 29.XI.2005, T. Pyrcz leg., [TWP]; 2 ♂♂: same locality, 11.II.2007, T. Pyrcz leg., 1 [MZUJ], 1 [UCD]; 8 ♂♂ and 1 ♀: Mérida, Mesa Alta, La Grita-Pregonero km33,5, bifurcation Bailadores vers Pregonero km 5-6, 2850 m, 29.XI.2005, P.Boyer leg.; 2 ♂♂: Mérida, Mesa Alta, Bailadores vers Pregonero km33,5, 5,5km après la jonction de La Grita, 2750 m, 2.XII.2005, P. Boyer leg., [PBF]; 1 ♀: Venezuela, Edos. Mérida – Táchira border, Bailadores – Pregonero, Mesa Alta, 2900-2950 m, 03.XII.2005, T. Pyrcz leg. [MZUJ].

#### DESCRIPTION

**MALE** (Fig. 1E): Head, thorax and abdomen as in the nominate subspecies. Wings: Size smaller than other subspecies, similar to *ioanae*; forewing length: 19-22 mm, mean: 19.8 mm, n=41. Forewing upperside uniform blackish-brown, turning a shade

lighter in older individuals, same as in the nominate or *valentinae*; three minute, white subapical dots in R5-M1, M1-M2 and M2-M3 apparent in all examined individuals, but as an average slightly smaller than in *valentinae*, and in some cases barely noticeable; two white postdiscal dots in M3-Cu1 and Cu1-Cu2, compared to one dot visible in *valentinae* or none in most individuals of the nominate or *giselleae*. Hindwing upper-side ground color blackish-brown, same as in the nominate subspecies or *valentinae*; a shining patch, quite variable in color, usually bluish-green with the greenish sheen slightly more noticeable than in *giselleae*, but never predominantly green as in the nominate or *valentinae*, marginally entering discal cell, in several examined individuals merely as sparse scales, reaching to tornus, and in some individuals extending slightly along outer margin, which is never the case for the nominate or *giselleae*. Forewing underside ground color slightly lighter than in the nominate subspecies and *giselleae*, with a yellow-brown suffusion in the median and postmedian area, particularly around the ocelli in M3-Cu1 and Cu1-Cu2 noticeably larger and more prominent than in the nominate subspecies or *giselleae*, and with a noticeable blackish suffusion of postdiscal and marginal areas in some individuals; otherwise similar to other subspecies. Hindwing underside ground color beige and sandy-brown, somewhat variable but the sandy suffusion is very prominent and in some individuals overcasts nearly the entire wing surface, except for an invariably lighter, whitish, postbasal and submarginal bands; darker brown ripple-like pattern of the nominate and *valentinae* not apparent similarly *giselleae*, otherwise similar to other subspecies. **Male genitalia** (Fig. 2C): Superuncus, valvae and gnathos longer and thinner than in the nominate subspecies, *giselleae* and *valentinae*; sub-scapium heavily sclerotized; saccus similar; dorsal process of the valvae shorter than ventral, curved downwards in the middle and covered with prominent spines in the apical half; apical part of ventral process slightly thicker and heavily covered with spines; aedeagus similar to the nominate and other subspecies.

**FEMALE** (Fig. 1F): Upperside ground color slightly lighter than in the male. Forewing length: 20-22 mm, mean: 21 mm, n=2 underside yellow-brown covering the entire wing surface. Hindwing underside nearly uniform yellow-beige, with a barely visible pattern of postbasal and median bands. **Female genitalia** (Figs. 3C1, 3C2) Papillae anales each with a small, strongly sclerotized navel-like protrusion. Ventral surface, between papillae anales, posterior to sclerotized plate of lamellae postvaginalis, constituting the dorsal wall of a small, wide batten, with delicate ribs converging anteriorly. Lamella postvaginalis with two shallow concavities. Lamella antevaginalis with a single, sharply ended protrusion pointing posteriorly. Ductus bursae short, approximately half the length of bursa copulatrix. Colliculum prominent. Ductus seminalis originating at ostium bursae. Bursa copulatrix rounded with two, short, approximately one-third the length of bursa, ribbon-like ostia. A prominent pointed process at the anterior edge of ostium bursae.

#### ETYMOLOGY

This subspecies is dedicated to Verónica SÁNCHEZ, a sister in law of the senior author.

*Lymanopoda marianna ioanae* PYRCZ, n. ssp.

(Figs. 1G, 1H, 2D)

## TYPE MATERIAL

HOLOTYPE ♂: Venezuela, Estado Táchira, El Batallón, Páramo El Rosal, carretera El Rosal – San José de Bolívar, 3000-3100 m, 01-02.XII.2005, T. Pyrcz leg., [MIZA]; Paratypes (7 ♂♂ and 2 ♀♀): same data as the holotype, 2 [TWP], 2 [MZUJ], 2 ♂ and 1 ♀: Táchira, Páramo El Rosal, La Grita vers San José de Bolívar km22, 3050 m, 01.XII.2005, P. Boyer leg., 1 ♂: same data but 3350 m, P. Boyer leg., [PBF]; 1 ♀: same locality and collector as the holotype, II.1996, [TWP];

## DESCRIPTION

MALE (Fig. 1G): Head, thorax and abdomen as in the nominate subspecies. Wings: Size same as *veronica*, smaller than the nominate and other subspecies; forewing length: 19-21 mm, mean: 19.8 mm; n=7. Forewing upperside uniform blackish-brown with a dark brown shade, very slightly lighter than in the nominate or *veronica*; three minute, white subapical dots in R5-M1, M1-M2 and M2-M3 apparent in all examined individuals, similar to *veronica*; two white postdiscal dots in M3-Cu1 and Cu1-Cu2, similar to *veronica*. Hindwing upperside ground color blackish-brown, same as on the forewing; a shining patch, somewhat variable in color, usually bluish-green with a greenish sheen slightly more noticeable than in *veronica* but never predominantly green as in the nominate or *valentinae*, not entering discal cell, contrary to *veronica* or other subspecies, and marginally entering the base of cell Cu1-Cu2, reaching to tornus, but never extending beyond vein Cu2. Forewing underside with the blackish suffusion of postdiscal and marginal areas generally heavier than in *valentinae*, otherwise similar to this subspecies, and differing from other subspecies in the same respect as *valentinae*. Hindwing underside color pattern quite variable but slightly more contrasting than in other subspecies, including *veronica*, which is reflected by the darker basal to median areas; the sandy suffusion generally less prominent than in *veronica*, otherwise similar; no darker ripple-like pattern characteristic to the nominate or *valentinae*. **Male genitalia** (Fig. 2D): Superuncus and gnathos shorter than in *veronica*, about the same length as in the nominate, uncus thinner than in the nominate subspecies, similar to *veronica*; sub-scapium heavily sclerotized; saccus slightly shallower than in the nominate or *veronica*; dorsal process of the valvae shorter than ventral, straight, covered with rather prominent spines in the apical half, however noticeably less so than *veronica*; ventral process thin and covered with rather small spines in the apical ¼; aedeagus similar to the nominate and other subspecies.

FEMALE (Fig. 1H): Upperside ground color slightly lighter than in the male. Forewing (length: 20.5 mm, mean: 20.5 mm, n=2) underside yellow-brown covering the entire wing surface. Hindwing underside nearly uniform yellow beige, with a barely visible pattern of postbasal and median bands. **Female genitalia** (not illustrated): Similar to that of *L. marianna veronica*.

## ETYMOLOGY

This subspecies is dedicated to Maite Ioana Sánchez RACHAUS, a sister in law of the senior author.

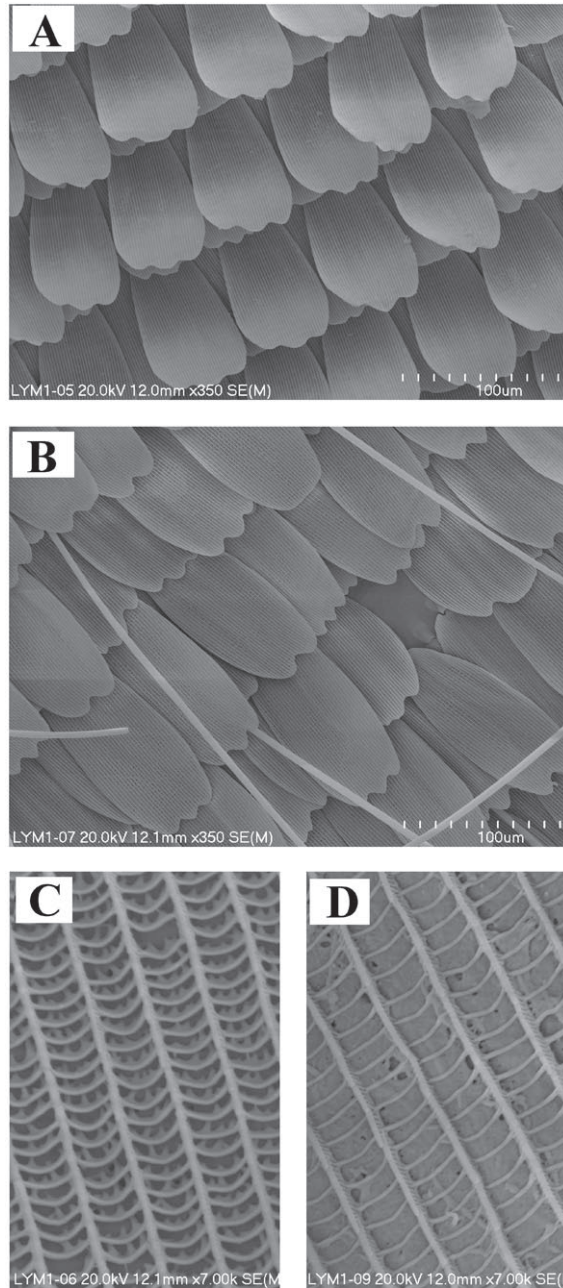
## SCALE MORPHOLOGY

HWD of *L. marianna* are covered with two main types of scales - brown and greenish-blue. Both types are oval/fusiform with a dentate terminus (some brown scales have rounded terminus). Brown scales are flat (Fig. 3B). Greenish-blue scales are markedly bent in the apical one-third (Fig. 3A). At the micromorphological level, the difference consist in that in greenish-blue scales the spaces between the cross ribs are filled by sponge-like nanoscaled material (Figs. 3C, 3D) (TILLEY & ELIOT 2002). This pepper-pot structure operates as a photonic band-gap material causing the increased reflectance in the spectral range from blue to near UV (VERTESY *et al.* 2004). The increased reflectance of blue is further enhanced by the curvature of scales terminus. Thus, three-dimensional scales of *Lymanopoda* and their nanostructure produce an intense greenish structural color. This kind of structural blue colour pattern is found in several species of the genus *Lymanopoda* including *L. samius* C. & R. FELDER, *L. hazelana* BROWN, *L. caeruleata* GODMAN & SALVIN, *L. cinna* GODMAN & SALVIN, *L. paisa* PYRCZ & RODRIGUEZ and an undescribed subspecies of *L. dietzi* ADAMS & BERNARD. Most of these species occur in the uppermost forest and forest-páramo ecotone. Forest structure at high elevations is characterized by lower tree cover, extremely dense understorey and abundant, tall bamboos. *Lymanopoda*, as well as other pronophilines fly mostly above the low canopy, contrary to their mid-elevation congeners. In such a habitat bright markings are particularly conspicuous. We argue that the blue color is a habitat driven adaptation and is functional in infraspecific communication, by facilitating mate locating and possibly playing a role in the courtship. Interestingly, it was observed, based on a large comparison material, that the green sheen tends to fade away in ageing individuals of *L. marianna* giving place to duller, plain blue color due to pterobilin, the blue pigment.

## BIONOMICS

*Lymanopoda marianna* is stenotopic, which is expressed by the narrow altitudinal range (2800-3300 m) and specific habitat. *L. marianna* is found in the forest - páramo ecotone, usually at the edge of forest gullies extending into lower paramo. It is always associated with tall *Chusquea* bamboos of the subgenus *Swallenchloa*, its host plant. Males of *L. marianna* patrol actively along high clumps of bamboo from around 0930 when weather conditions are favorable, that is only during periods of bright sunshine. Activity switches into predominantly perching around 1300-1400. Mate locating and patrolling is shorter whenever weather is particularly warm and dry, and may end even before 1130. Males fly generally along well established pathways, and occasionally engage into short checking activity with other co-specifics, but aerial combats have not been observed. Individuals occasionally fly low above the ground, but generally





3. Scales (SEM): **A.** *Lymanopoda marianna veronicae* (blue scales, folded); **B.** *Lymanopoda m.a veronicae* (brown scales, flat); **C.** *Lymanopoda m. veronicae* (blue scale, detail); **D.** *Lymanopoda m. valentinae* (brown scale, detail)

only when crossing above grassland from one area of bamboo thickets to another. In the early afternoon, during sunny days, males quite often come to the ground to feed on decomposing animal matter and moisture. The behaviour of *L. marianna* is similar to that of other species of *Lymanopoda* occurring in the uppermost forest and lower páramo, especially the blue *L. samius* WESTWOOD in the Colombian Eastern Cordillera and *L. hazelana* BROWN in Ecuador. Females of *L. marianna* are seldom observed, mostly because they are less active. They are usually seen when carrying out short flights in search of appropriate host plants. Oviposition takes place on young leaves, and eggs, as far as was observed, are glued singly on their ventral side. Courtship was not observed. In some places *L. marianna* is relatively common in its habitat (Mesa Alta, Qda. Ranchería), and as many as 30 individuals could be observed within an hour. Flight period corresponds usually to the end of the rainy season, November-January, but scattered individuals can be observed throughout the year.

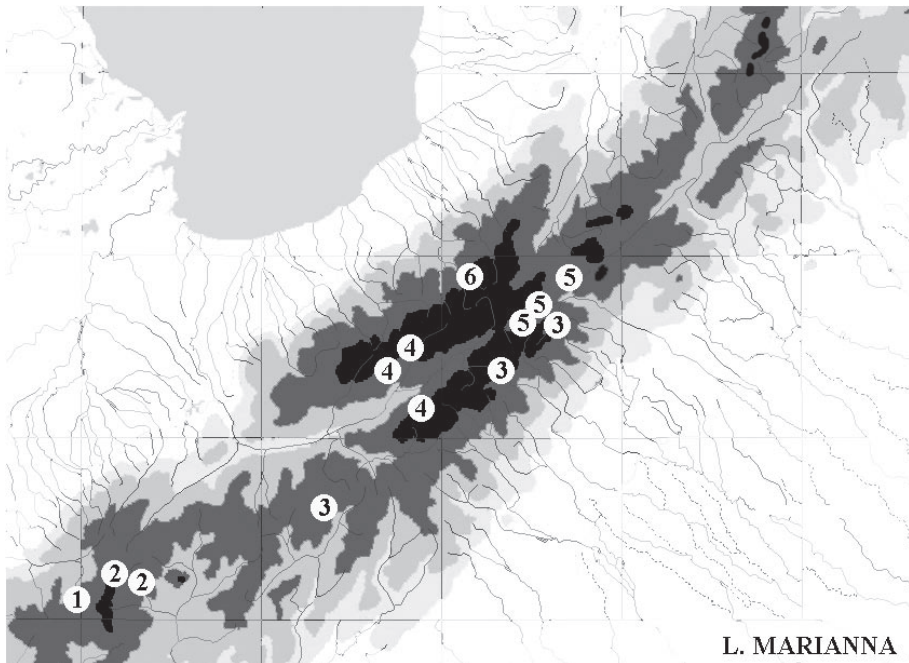
#### DISTRIBUTION PATTERNS

Our study confirms that *Lymanopoda marianna* is endemic in the Venezuelan Cordillera de Mérida. It is one of the five species of the genus *Lymanopoda* found in this Andean range, out of a total of approximately 60 species (LAMAS *et al.* 2004; PYRCZ 2004). Apart from *L. marianna*, three widespread species (*L. obsoleta* (WESTWOOD), *L. albocincta* HEWITSON and *L. caucana* WEYMER) and one endemic (*L. dietzi*) occur in the CM.

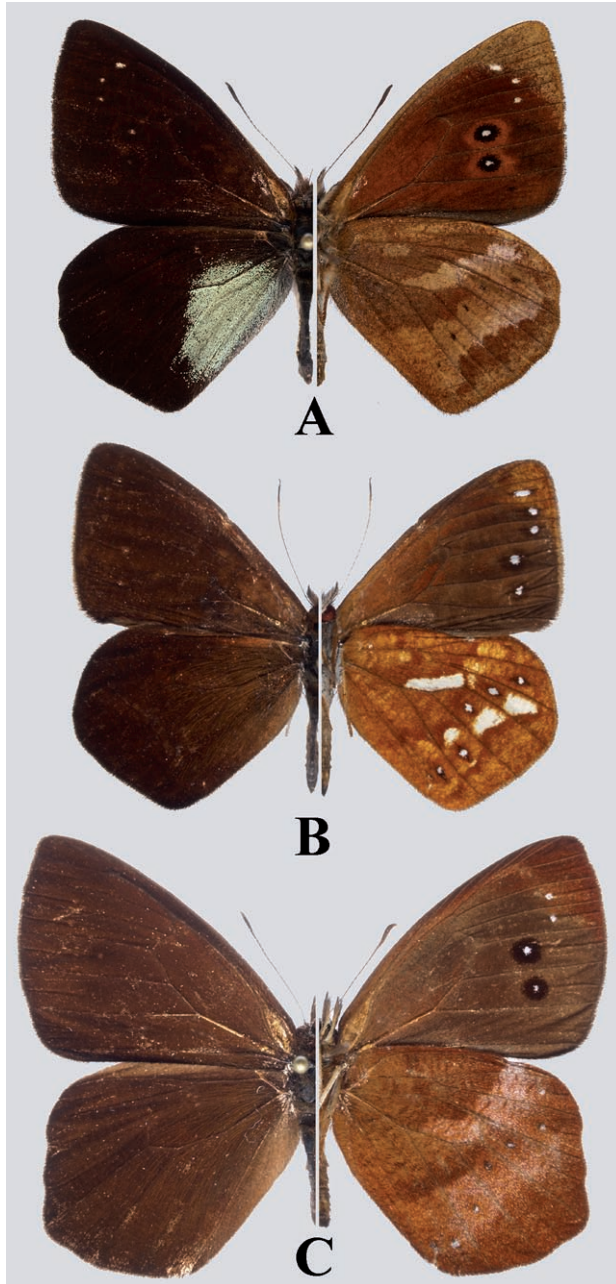
*L. marianna* has been located in the central and southern part of the range (Fig. 4). It appears to be absent from the entire northern CM, including the north-central Niquitao, Guaramacal and Cendé massifs. The nominate subspecies was described from the area of the town of Mérida. The types come most probably from the valley of La Pedregosa, a well-known collecting locality of Briceño, STAUDINGER'S provider of butterflies from Mérida. *L. marianna marianna* occurs in the valley of Chama on its northern La Culata and southern Sierra Nevada slopes. *L. marianna valentinae* is apparently restricted to the valley of the Río Santo Domingo and its affluent, Río Ranchería. The nominate and *valentinae* are recognized from other subspecies by the green (not greenish-blue) HWD patch. *L. marianna jacquelineae* was found on the north-western, Lago de Maracaibo slopes of La Culata. Higher elevations on these slopes of the CM have not been sampled except for the type locality of *jacquelineae*. This area is not topographically or ecologically isolated as are the valleys of Chama or Santo Domingo and there are no ecological barriers along the western slopes of the CM, so the range of *jacquelineae* could well extend to the South. The nominate and *jacquelineae* are the subspecies with the largest HWD patch, and the only ones with HWD patch entering discal cell. *L. marianna ioanae* is apparently effectively restricted to the southern slopes of the Batallón massif, since on the northern slopes of the same it is replaced by *veronica*. The two southern subspecies are recognized by the noticeably smaller size (expressed in the FW length). There is apparently no solid spatial isolation between *ioanae* and *marianna* since in some localities (Las Antenas, Quebrada de Los Píos) the two subspecies probably hybridize (intermediate phenotypes were observed), which results in

intermediate phenotypes. *L. marianna giselleae* has the widest observed range of all the subspecies. It occurs along the eastern, Los Llanos slopes of the CM and was detected from Páramo de San José in the South to the El Hatico range in the North. There is some clinal variation between the populations of *giselleae*, which is expressed in the somewhat lighter ground colour of northern specimens, but otherwise, the diagnostic characters of *giselleae* are found in all the localities. In the El Hatico range locally *giselleae* is found within the Santo Domingo valley, and occurs parapatrically with *valentinae*. The nearest known localities of the two subspecies are less than a kilometre away, and they are not separated ecologically or topographically. Yet, there appears to be no hybridizing between the two, as intermediate phenotypes have not been detected, whereas colour patterns of the two subspecies are sharply different.

Based on morphological features, the affinities between the subspecies can be preliminarily evaluated. A cladistic analysis assessing the relations between the subspecies based exclusively on morphology is methodologically unreliable considered their phyletic closeness and possible homoplasies, therefore it is not carried out herein. Colour pattern (HWD greenish-blue patch size and shape, HWV postdiscal and sub-marginal bands, and “ripple” pattern, FWD ground colour) segregate the subspecies of *L. marianna* into two groups. South-eastern subspecies *veronica*, *ioanae* and *giselleae* on the one hand, and central-north-western *marianna*, *valentinae* and *jacquelineae* on the other cluster together. A comparison of male genitalia is less conclusive pointing



4. Map (distribution of the subspecies of *Lymanopoda marianna*): 1. *L. marianna ioanae*; 2. *L. m. veronicae*; 3. *L. m. giselleae*; 4. *L. m. marianna*; 5. *L. m. valentinae*; 6. *L. m. jacquelineae*

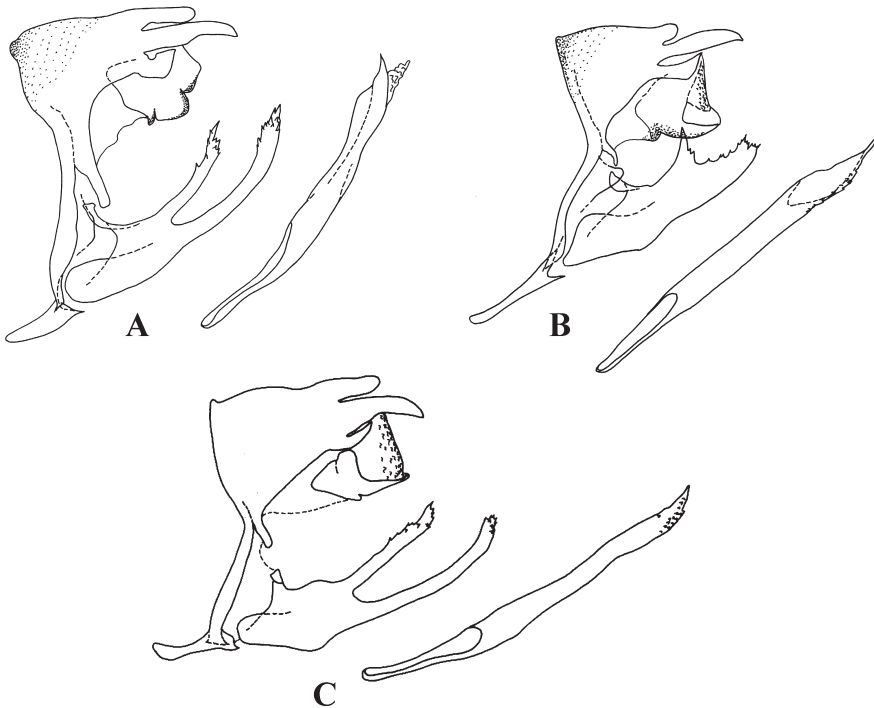


5. Adults (left: dorsum/ right: venter): **A.** *Lymanopoda marianna veronicae* (paratype); **B.** *Lymanopoda lebbaea* (Betania, Táchira, Venezuela); **C.** *Lymanopoda obsoleta* (Cachiyacu-Casca, Junín, Peru)

out an affinity between *veronica* and *jacquelineae* both marked by the shorter dorsal process than the ventral, thickened in apical part with prominent spines along dorsal edge. Females are known for three subspecies only so their genitalia could not be compared so far. Based on this, a biogeographic pattern is apparent. It correlates the centers of endemism with two main topographic isolates within the range (central Sierra Nevada/La Culata and southern Batallón/La Negra) which is congruent with the distribution patterns of the genera of Pronophilini occurring in the subpáramo and páramo of the CM, *Redonda*, *Steromapedaliodes* and *Diaphanos* (VILORIA *et al.* 1993; VILORIA 1994; VILORIA & PYRCZ 2001; VILORIA *et al.* 2004). However, it yields another result, the existence of a western-eastern slopes pattern, pointing out the isolating role of the main ridge of the CM. It is a novelty in the biogeography of cloud forest species of the CM. Also, the Santo Domingo valley (*valentinae*) is recognized for the first time as an area of endemism.

#### AFFINITIES AND PHYLOGENY

The affinities of *Lymanopoda marianna* are evaluated based on adult morphology, including wing colour patterns, male and female genitalia, and on molecular data.

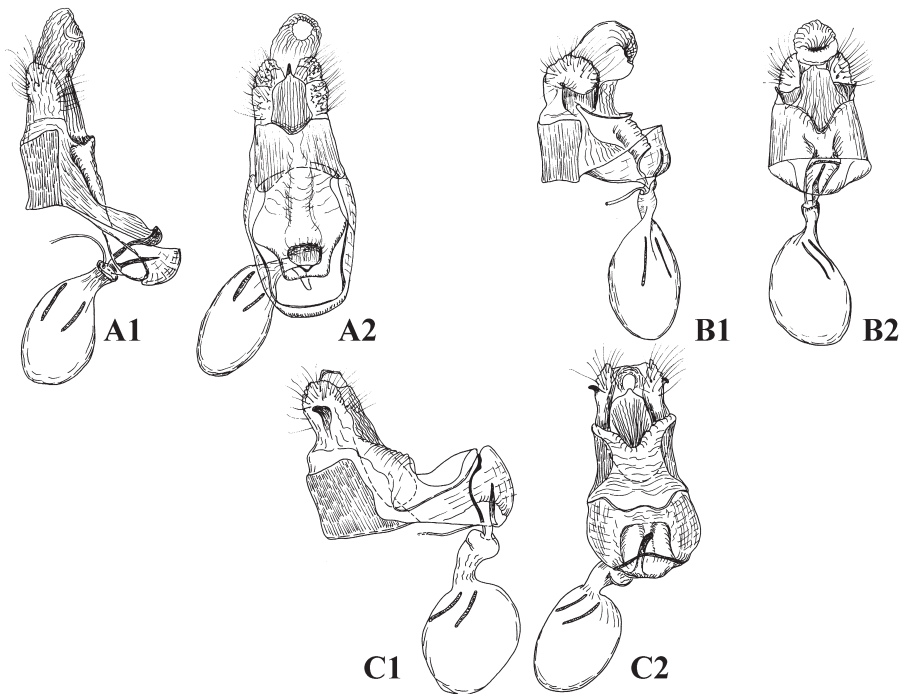


6. Male genitalia (in lateral view): **A.** *Lymanopoda obsoleta* (Cachiyacu-Casca, Junin, Peru); **B.** *Lymanopoda lebbaea* (Betania, Táchira, Venezuela); **C.** *Lymanopoda marianna marianna* (La Culata, Mérida, Venezuela)



Wing shape and colours pattern of *L. marianna* indicate a close affinity with *L. lebbaea* C. & R. FELDER (Fig. 5B) found throughout EC. Particularly, the HWV pattern, which is considered as providing solid phylogenetical characters (PYRCZ *et al.* 1999), is closely similar in the two species. White maculae in discal cell and postdiscally, present in *L. lebbaea* and absent in *L. marianna*, are highly variable, in some species infrasubspecifically. *L. obsoleta* (Fig. 5C) and allied species (*L. confusa* BROWN, *L. altis* WEYMER, *L. lecromi* PYRCZ & VILORIA) are in this respect completely dissimilar, with an acute or falcate FW apex, square HW, and distinctive HWV pattern. The greenish-blue HWD patch of *L. marianna*, which is a conspicuous element of the colour pattern, seems without any phyletic value. It is found in several loosely related species, according to data based on adult morphology and DNA, as listed earlier.

Male genitalia of *L. marianna* are characterised by the narrow valvae extending into two long, roughly parallel, narrow, apically dentate processes. They are closely similar to the genitalia of *L. obsoleta* (WESTWOOD). This group and the related group of *L. panacea* (HEWITSON) are recognized from other clades of *Lymanopoda* by this apparently synapomorphic feature (PYRCZ 2000). In *L. lebbaea* the dorsal process is

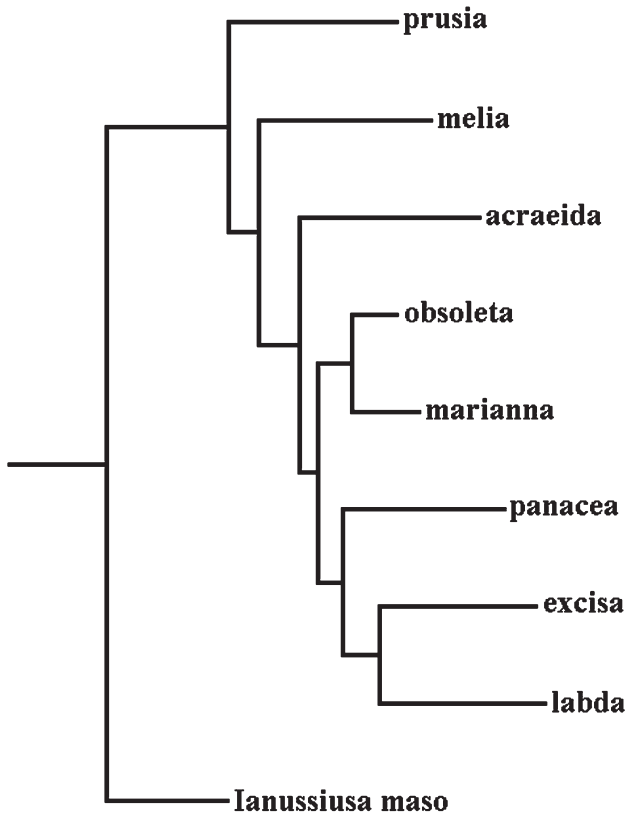


7. Female genitalia (in ventral and ventral view): A1. *Lymanopoda obsoleta* lateral (Monte Zerpa, Mérida, Venezuela); A2. *Lymanopoda obsoleta* ventral (Monte Zerpa, Mérida, Venezuela); B1. *Lymanopoda lebbaea* lateral (vía Páramo El Tamá, Táchira, Venezuela); B2. *Lymanopoda lebbaea* ventral (vía Páramo El Tamá, Táchira, Venezuela); C1. *Lymanopoda marianna veronicae* lateral (paratype); C2. *Lymanopoda m. veronicae* ventral (paratype)



considerably shorter, teeth-like pointing upwards, whereas the apical part is massive with strongly dentate dorsal surface. In *L. marianna* and *L. obsoleta* superuncus is longer than in *L. lebbaea*. Additionally, pedunculus is considerably longer in the former two species. On the other hand, saccus is much deeper in *L. lebbaea* (Fig. 6).

Female genitalia of *L. marianna* show close similarity to *L. lebbaea* and important differences compared to *L. obsoleta*. *L. obsoleta* differ chiefly from *L. marianna* and *L. lebbaea* in the arrangement of the sclerotized plates of eighth abdominal segment of both sternite and tergite. Due to the large size of lamella antevaginalis and lamella postvaginalis constituting the sterigma, its sinus vaginalis is widely open and the position of its concave anterior wall in relation to the tergite is shifted anteriorly. This affects the position of the long axis of ductus bursae and bursa copulatrix, which are fixed at the bottom of sterigma at about 45° to the long axis of the abdomen. Laterally, sterigma is framed with long, thin, gradually narrowing sclerites connecting with eighth tergite. Contrary to *L. obsoleta*, the opening leading to sinus vaginalis in *L. marianna* and *L. lebbaea* is considerably narrower and the long axis of ductus bursae and bursa copulatrix is at a right angle to the long axis of the abdomen. Narrowing sclerites of



8. *Lymanopoda* phylogeny (partial)

sterigma connecting with eight tergite are short and laterally wide. In *Lymanopoda marianna* and *L. lebbaea* there are small sclerotized lateral bumps on papillae anales, which are lacking in *L. obsoleta* (Fig. 7).

According to all trees - individual gene trees, concatenated nuclear genes + mtDNA, and all genes concatenated - *L. marianna* is a basal member of the *L. obsoleta* clade, which also includes *L. dietzi*, *L. altis*, *L. confusa* and *L. magna*. The phylogeny based on concatenation of all genes shows the major clades of *Lymanopoda* and the relative placement of *L. marianna* (Fig. 8). Accordingly and supported by the other trees, *L. labda* HEWITSON (a closely related allopatric west slopes EC replacement of *L. lebbaea*) and other members of this large clade are distant from the *L. obsoleta* group (CASNER, in prep). The relative placement of clades varied among gene trees and concatenation methods, and therefore deeper relationships cannot be inferred.

#### CONCLUSION

This study pinpoints an interesting incongruence between two data sets. Colour patterns and female genitalia indicate that *L. marianna* is closely related to the *L. lebbaea* species group (including *L. labda* and *L. nadia* PYRCZ). On the other hand, male genitalia and DNA evidence clearly place *L. marianna* in the *L. obsoleta* clade. Although deeper branching events are unresolved from our molecular analyses, adult morphology and all gene trees agree that the *L. lebbaea* clade and *L. obsoleta* clade are distantly related. Our current understanding of the evolution of morphological characters puts forth two explanations. One, it is possible that *L. marianna* belongs with the *L. obsoleta* clade, which is congruent with the male genitalic morphology and molecular results, and the female genitalia and wing pattern have undergone dramatic divergence, setting it apart from the rest of the clade. However, this does not explain the far reaching convergence of female genitalia and colour patterns with *L. lebbaea*. The convergent colour pattern is especially unlikely in light of the fact that *L. marianna* and *L. lebbaea* are not geographically sympatric. Another explanation is that the *L. marianna* actually belongs in the *L. lebbaea* clade and the structure of the male genitalia is a homoplasy. This, however stands in sharp contradiction with the phylogeny constructed on DNA data putting *L. marianna* in the *L. obsoleta* clade. Thus, our results present a logical dilemma, at present not resolved in a satisfactory manner.

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## REFERENCES

- ADAMS, M. J., BERNARD, G. I., 1981. Pronophilinae butterflies (Satyridae) of the Cordillera de Mérida, Venezuela. *Zool. Journ. Linn. Soc.*, **71**: 343-372.
- D'ABRERA, B., 1988. Butterflies of the Neotropical Region. Part V. Nymphalidae (Conc.) & Satyridae. Victoria, Black Rock, Hill House, [viii] + 679-877.
- GAEDE, M., 1931. Satyridae. II. In: STRAND, E. (Ed.): *Lepidopterorum Catalogus*, 29(46): 321-544.
- JUDZIEWICZ, E. J., CLARK, L. G., LONDOÑO, X., STERN, M. J., 1999. American bamboos. Smithsonian Institution Press, Washington and London, 392 pp.
- JUDZIEWICZ, E. J., RIINA, R. 2005. *Aulonemia dinirensis* (Poaceae: Bambusoideae: Bambuseae) a new dwarf Venezuelan species from the easternmost Andean páramos. *Journ. Amer. Bamboo Soc.*, **19**(1): 11-15.
- KLOTS, A. B., 1956. Lepidoptera. In: TUXEN, S. L. (Ed.), *Taxonomists' Glossary of Genitalia in Insects*. Munksgaard, Copenhagen, pp. 97-110.
- LAMAS, G., VILORA, A. L., PYRCZ, T. W., 2004. Subtribe Pronophilina. In: E. LAMAS (Ed.), *Atlas of Neotropical Lepidoptera, Checklist: Part 4A, Hesperoidea – Papilionoidea*. Association for Tropical Lepidoptera/Scientific Publishers, Gainesville, pp. 206-215.
- PEÑA, C., WAHLBERG, N., WEINGARTNER, E., KODANDARAMAIAH, U., NYLIN, S., FREITAS, A. V. L., BROWER, A. V. Z., 2006. Higher level phylogeny of Satyrinae butterflies (Lepidoptera: Nymphalidae) based on DNA sequence data. *Molecular Phyl. Evol.*, **40**: 29-49.
- PYRCZ, T. W., 1995. A new genus, *Tamania* and a new species, *Tamania jacquelineae* from the Tamá range, Venezuela - Colombia border (Satyridae: Pronophilini). *Lambillionea*, **95**(4): 519-525.
- , 2000. Rewizja zoogeograficzna i taksonomiczna rodzaju *Lymanopoda* (Lepidoptera, Nymphalidae, Satyrinae). Instytut Zoologiczny Uniwersytetu Jagiellońskiego, PhD Thesis.
- PYRCZ, T. W., VILORIA, A. L., 2009. A. L. Systematics, zoogeography and bionomics of high Andean pedalioidines, Part 5: A new subspecies of *Pedaliodes ornata* STAUDINGER from the Cordillera de Merida (Lepidoptera: Nymphalidae: Satyrinae). *Genus, Wrocław*, **20**(1): 13-22.
- PYRCZ, T. W., WOJTUSIAK, J., 2002. The vertical distribution of pronophilina butterflies (Nymphalidae, Satyrinae) along a elevational transect in Monte Zerpa (Cordillera de Mérida, Venezuela) with remarks on their diversity and parapatric distribution. *Global Ecol. Biogeogr.*, **11**: 211-221.
- PYRCZ, T. W., WILLMOTT, K., HALL, J., 1999. Contributions to the knowledge of Ecuadorian Pronophilini, Part 3, three new species and five new subspecies of *Lymanopoda*, *Genus, Wrocław*, **10**(3): 497-522.
- SALGADO-LABOURIAU, M. L., 1979. El medio ambiente páramo. Centro de estudios avanzados, IVIC.
- SCHWANWITSCH, B., 1924. On the groundplan of the wing-pattern in nymphalids and certain other families of rhopalocerous Lepidoptera. *Proc. Zool. Soc. London*, **34**: 509-528.
- STAUDINGER, O., 1897. Neue südamerikanische Tagfalter. *D. Entomol. Zeitschr. „Iris“*, **10**(1): 123-151, pls. 5-8.
- TILLEY, R. J. D., ELIOT, J. N., 2002. Scale microstructure and its phylogenetic implications in lycaenid butterflies (Lepidoptera, Lycaenidae). *Trans. Lepidopter. Soc. Japan*, **53**: 153-180.
- VEILLON, J-P., 1989. Los bosques naturales de Venezuela, Parte I, El medio ambiente. Mérida, Universidad de Los Andes.
- VERTESY, Z., BALINT, ZS., KERTESZ, K., MEHN, D., KIRICSI, I., LOUSSE, V., VIGNERON, J-P., BIRÓ, L. P., 2004. Modifications to wing scale microstructures in Lycaenid butterflies. *Microscopy and Analysis*, **18**(4): 25-27.
- VILORIA, A. L., 1994. High Andean Pronophilini from Venezuela: Two new species of Diaphanos (Nymphalidae: Satyrinae). *Journ. Lepidopter. Soc.*, **48**(3): 180-189.
- , 2003. Historical biogeography and the origins of the satyrine butterflies of the tropical Andes (Lepidoptera: Rhopalocera). In: J. J. MORRONE and J. LLORENTE (Ed.), *Una perspectiva latinoamericana de la*

- biogeografía.(Ed.), Una perspectiva latinoamericana de la biogeografía. Universidad Autónoma de México, México.
- VILORIA, A. L., PYRCZ, T. W., 2001. Revalidación y revisión de *Steromapedaliodes* Forster, con descripción de dos especies nuevas (Lepidoptera: Nymphalidae, Satyrinae). *Anartia*, **15**: 1-2.
- VILORIA, A. L., PYRCZ, T. W., CAMACHO, J., 1993. Sistemática de los Satyridae de media y alta montaña (Pronophilini) y la determinación de regiones de endemismo en el territorio venezolano. Resúmenes del V Congreso Latinoamericano y XIII Venezolano de entomología, 226-227.
- VILORIA, A. L., PYRCZ, T. W., WOJTUSIAK, J., FERRER-PARIS, J. R., BECCALONI, G. W., SATTLER, K., LEES, D., 2004. The first case of braquiaptery in butterflies, *Proc. R. Soc. Lond. B (Suppl.)* **270**, S21-S24, DOI 10.1098/rsbl.2003.0015.
- WEYMER, G., 1911. 4 Familie: Satyridae. In: SEITZ, A. (ed.): *Die Gross-Schmetterlinge der Erde*, **2**; Exotische Fauna, 5. Stuttgart: A. Kernen, pp. 173-283.

## APPENDIX 1

### Coordinates of collecting sites

1. El Potrero vía Torondoy, Timotes, 2900-3100 m (08°56'56"N / 70°56'21"W);
2. Ranchería, Pueblo Llano, 2900-3000 m (08°59'16"N / 70°37'11"W);
3. El Baho, Santo Domingo, 2600-3200 m (08°50'13"N / 70°42'30"W);
4. Los Frailes, Santo Domingo, 2850-2950 m (08°48'53"N / 70°46'25"W);
5. La Culata, Río Mucujún, 3100-3300 m (08°45'14"N / 71°03'31"W);
6. Monte Zerpa, Río Albarregas, 2450-3100 m (08°40'15"N / 71°09'17"W);
7. La Mucuy vía Laguna Verde, Sierra Nevada, 2450-2950 m (08°36'24"N / 71°01'38"W);
8. La Aguada - Loma Redonda, Sierra Nevada, 3250-3400 m (08°33'37"N / 71°05'11"W);
9. Páramo de San José, San José, 2900-3100 m (08°20'09"N / 71°18'00"W);
10. Qda. De Los Píos, Batallón, 2900-2950 m (08°10'38"N / 70°53'42"W);
11. Mesa Alta, Batallón, 2750-2900 m (08°10'15"N / 71°42'57"W);
12. La Antena, Batallón, 2900-3250 m (08°09'24"N / 71°54'16"W);
13. Páramo El Rosal, Batallón, 2900-3200 m (08°01'05"N / 71°58'16"W);
14. Los Morritos, Sierra Nevada, 2900-3300 m (08°42'40"N / 70°46'10"W).

## APPENDIX 2

**Original description of *Lymanopoda marianna*** (translated from German): „I received two specimens of this new species, which, alongside *Oxeoschistus opalinus* was collected in the high mountains near Mérida (Venezuela). The pattern of the wings upperside of this species is very similar to the aforementioned species. Wings span: 36 and 40 mm. The upperside is blackish-brown. Three subapical spots on the forewing. Hindwings with a large, golden green patch along the inner margin, which also fills the lower half of discal-cell. Forewing underside dark chestnut-brown with a light brown-yellow apical part, basad with three white dots and two ocelli with white pupils on both sides of third median vein. Hindwing underside brown-yellow, marbled with two dark (brown) and two lighter (white-grey) bands and 4-5 small, black ocelli with white pupils in distal area. A more precise description is not required considered the excellent quality of the illustration. I think that the beautiful shining golden-green patch along the inner margin, as with the previous species, cannot be more clearly presented. On the forewing underside two ocelli, one under the other ringed with light brown (replacing the lacking white pupil). Forewing underside in the illustrated, smaller male are slightly lighter than in the larger male, which has an additional basal patch near costa and in the postmedian area five (instead of four) white ocelli with minute black ring. Black antennae have (towards base) conspicuous, light (white) rings. Palpi are (hairy) light, alternately dirty grey-brown and black, on the ventral side in the apical part nearly all black. Thorax and legs, covered with long hair, are light dirty-brown (brown-yellow). Abdomen dark covered ventrally with light grey hair.”

## APPENDIX 3

Vou. ID	genus	sp. / ssp.	country	locality	elevation	coll. date
KA 200	<i>Lymanopoda</i>	<i>prusia</i>	Peru	San Luis, Cuzco	2800	20.09.2008
KA 201	<i>Lymanopoda</i>	<i>prusia</i>	Peru	San Luis, Cuzco	2800	20.09.2008
KA 139	<i>Lymanopoda</i>	<i>melia</i> ssp.	Ecuador	San Borja, Tungurahua	3200	19.01.2005
KA 140	<i>Lymanopoda</i>	<i>elia</i> ssp.	Ecuador	San Borja, Tungurahua	3200	19.01.2005
KA 205	<i>Lymanopoda</i>	<i>acraeida acraeida</i>	Peru	Wayqecha, Cuzco	14000	10.09.2008
KA 206	<i>Lymanopoda</i>	<i>acraeida acraeida</i>	Peru	Wayqecha, Cuzco	1400	10.09.2008
KA 3	<i>Lymanopoda</i>	<i>obsoleta</i>	Peru	San Luis, Cuzco	2500- 3000	22.02.2005
KA 6	<i>Lymanopoda</i>	<i>obsoleta</i>	Peru	Aquele, Puno	2300	02.02.2005
KA 9	<i>Lymanopoda</i>	<i>obsoleta</i>	Peru	Aquele, Puno	2300	02.02.2005
KA 12	<i>Lymanopoda</i>	<i>obsoleta</i>	Venezuela	El Baho, Merida	2400	14.02.2007
KA 13	<i>Lymanopoda</i>	<i>obsoleta</i>	Venezuela	Monte Zerpa, Merida	2500- 2760	05.02.2007
KA 14	<i>Lymanopoda</i>	<i>obsoleta</i>	Venezuela	Monte Zerpa, Merida	2500- 2760	05.02.2007
KA 15	<i>Lymanopoda</i>	<i>obsoleta</i>	Venezuela	Monte Zerpa, Merida	2500- 2760	05.02.2007
KA 16	<i>Lymanopoda</i>	<i>obsoleta</i>	Venezuela	La Mucuy, Merida	2500	07.02.2007
KA 44	<i>Lymanopoda</i>	<i>obsoleta</i>	Ecuador	Loja-Zamora, Zamora-Ch.	2060	13.12.2006
KA 45	<i>Lymanopoda</i>	<i>obsoleta</i>	Ecuador	El Tablon, Tungurahua	2700	13.11.2006
KA 46	<i>Lymanopoda</i>	<i>obsoleta</i>	Ecuador	El Tablon, Tungurahua	2700	10.11.2006
KA 76	<i>Lymanopoda</i>	<i>obsoleta</i>	Ecuador	Runtun, Tungurahua	2850	02.11.2006
KA 77	<i>Lymanopoda</i>	<i>obsoleta</i>	Ecuador	Runtun, Tungurahua	2851	03.11.2006
KA 79	<i>Lymanopoda</i>	<i>obsoleta</i>	Ecuador	El Tablon, Tungurahua	2700	11.10.2006
KA 81	<i>Lymanopoda</i>	<i>obsoleta</i>	Ecuador	El Tablon, Tungurahua	2700	10.11.2006
KA 83	<i>Lymanopoda</i>	<i>obsoleta</i>	Ecuador	El Tablon, Tungurahua	2700	13.11.2006
KA 120	<i>Lymanopoda</i>	<i>obsoleta</i>	Colombia	Lara, B Aives, Lende	2100	28.08.2007
KA 121	<i>Lymanopoda</i>	<i>obsoleta</i>	Colombia	Guame, Antioquia	2600	08.09.2003
KA 148	<i>Lymanopoda</i>	<i>obsoleta</i>	Peru	San Luis, Cuzco	3000	11.09.2007

## APPENDIX 3 (continuation)

KA 149	<i>Lymanopoda</i>	<i>obsoleta</i>	Peru	Mendoza, Amazonas	2200	03.08.2007
KA 150	<i>Lymanopoda</i>	<i>obsoleta</i>	Venezuela	C.Tovar, Aragua	2100	25.02.2007
KA 186	<i>Lymanopoda</i>	<i>obsoleta</i>	Peru	Milpo, Pasco	2600	22.08.2007
KA 187	<i>Lymanopoda</i>	<i>obsoleta</i>	Peru	Milpo, Pasco	2600	22.08.2007
KA 188	<i>Lymanopoda</i>	<i>obsoleta</i>	Peru	San Luis, Cuzco	2460- 2700	13.09.2007
KA 189	<i>Lymanopoda</i>	<i>obsoleta</i>	Peru	San Luis, Cuzco	2460- 2700	13.09.2007
KA 190	<i>Lymanopoda</i>	<i>obsoleta</i>	Peru	San Luis, Cuzco	2460- 2700	12.09.2007
KA 191	<i>Lymanopoda</i>	<i>obsoleta</i>	Venezuela	Colonia Tovar, Aragua	2100	25.02.2007
KA 192	<i>Lymanopoda</i>	<i>obsoleta</i>	Peru	San Luis, Cuzco	2460- 2700	11.09.2007
KA 202	<i>Lymanopoda</i>	<i>obsoleta</i>	Peru	Molinopampa, Amazonas	2870	19.09.2008
KA 203	<i>Lymanopoda</i>	<i>obsoleta</i>	Peru	Molinopampa, Amazonas	2870	19.09.2008
KA 204	<i>Lymanopoda</i>	<i>obsoleta</i>	Peru	Molinopampa, Amazonas	2870	20.09.2008
KA 41	<i>Lymanopoda</i>	<i>marianna veronicae</i>	Venezuela	Pmo. de Batallon, Merida	2900	10.02.2007
KA 160	<i>Lymanopoda</i>	<i>marianna marianna</i>	Venezuela	La Culata, Merida	2950	07.02.2006
KA 56	<i>Lymanopoda</i>	<i>panacea panacea</i>	Ecuador	San Francisco, Zamora-Ch.	2100	05.11.2006
KA 60	<i>Lymanopoda</i>	<i>excisa browni</i>	Ecuador	Saraguro, Loja	3025	04.11.2006
KA 61	<i>Lymanopoda</i>	<i>excisa browni</i>	Ecuador	Saraguro, Loja	3025	04.11.2006
KA 62	<i>Lymanopoda</i>	<i>labda ssp.</i>	Ecuador	Yanayacu, Napo	2100	22.11.2006
KA 63	<i>Lymanopoda</i>	<i>labda ssp.</i>	Ecuador	Yanayacu, Napo	2100	22.11.2006
KA 108	<i>Lymanopoda</i>	<i>labda labda</i>	Colombia	El Retiro, Antioquia	2700	10.08.2007
KA 109	<i>Lymanopoda</i>	<i>labda labda</i>	Colombia	El Retiro, Antioquia	2700	10.08.2007
KA 198	<i>Ianussiusa</i>	<i>maso ssp.</i>	Colombia	El Retiro, Antioquia	2700	08.08.2007